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Pleistocene marine fish invasions and paleoenvironmental reconstructions in the eastern Mediterranean

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ABSTRACT

Marine bioinvasions affect ecosystems in irreversible ways, creating socio-economic problems worldwide. In particular, eastern Mediterranean marine fish faunas today are significantly disturbed due to overfishing, habitat deterioration, the Lessepsian invasion, and climate change. Isolating the impact of each parameter is difficult, because pre-anthropogenic activity data are lacking. In this study, we use the paleontological record to infer the causes and mechanisms behind marine fish invasions, focusing on the Mediterranean basin, which is a restricted basin and a biological hotspot, where the effects of climatic and oceanographic changes are amplified. Therefore, the Mediterranean Sea is an ideal area to study marine biological invasions in relation to abrupt climate changes. Furthermore, we focus on the Pleistocene, which was a period of intense glacial–interglacial changes. Thus, we investigate the effect of climate changes on the fish fauna of an eastern Mediterranean shelf, by identifying the fish otoliths in the Early–Middle Pleistocene marine sediments of Rhodes (Greece). We offer a synthesis of the Mediterranean marine fish from the Tortonian until today and hypothesize on the conditions that drove marine fish distribution range shifts during the Pleistocene. We reconstruct the paleobathymetric evolution of the study areas based on fish otoliths, and we consider taphonomy in our interpretations. The Pleistocene climatic variability induced periodic and gradual replacements of fish taxa. Episodic invasions of cold-water North Atlantic mesopelagic species are correlated with intervals of climatic deterioration, specifically during marine isotope stages 50, 44, 36, 20, and 18.

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1. Introduction

Marine ecosystems worldwide are severely disturbed by biological invasions, with direct socio-economic implications for their dependent human populations (Pauly et al., 2005; Byrnes et al., 2007; Early et al., 2016; Dawson et al., 2017; Seebens et al., 2017). This phenomenon is especially intense in the eastern Mediterranean Sea, where alien marine species increasingly invade Mediterranean waters from the Red Sea via the Suez Canal (Lessepsian invasion) and the Atlantic Ocean (Galil et al., 2015; Rilov, 2016; Piroddi et al., 2017).

Marine fish invasions are a major issue with the present-day global warming (Perry et al., 2005; Pörtner and Knust, 2007; Walther et al., 2009; Cheung et al., 2009; Comte and Olden, 2017). Fish are strongly affected by climatic and oceanographic changes (Rose, 2005), through processes (such as distribution shifts, lifestyle adaptations, extinctions, and morphological modifications) that are not well-known and species-specific. In the Mediterranean, in particular, the distribution of pelagic fish in the western, central, and eastern parts of the basin has been linked to different modes of climatic variability (Tsikliras et al., 2018). Moreover, geographic boundaries, such as sills, may restrict the distribution of deep-water demersal species, but not those of pelagic and mesopelagic

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species that could be affected by the chemical and physical parameters of the seawater masses. In order to distinguish between the effects of these processes, we turn to the geological past, as a source of paleodiversity data that is: a) undisturbed by human activity and b) encompasses a much longer record including extreme climatic variations.

What was the imprint of past biological invasions on the fossil record? Paleontological data suggest that distribution range shifts due to environmental changes such as the ones observed today were common in the past (e.g., Enquist et al., 1995; Jablonski et al., 2006, 2013; Peterson and Lieberman, 2012; Palcu et al., 2017). In order to detect past marine biological invasions, in particular Atlantic marine species invading eastern Mediterranean waters, we synthesize and examine the Pleistocene evolution of the marine fish fauna in the area, because intense environmental changes took place during this Epoch due to glacial–interglacial successions, and it is therefore a good candidate for marine species invasions in the Mediterranean Sea. Moreover, we identify the fish otolith assemblages in the early–middle Pleistocene (Gelasian to Ionian) hemipelagic sediments of the island of Rhodes (Greece; Fig. 1). Rhodes is of particular interest, because Pleistocene coastal to deep sea sediments have been uplifted there and are presently well-exposed onshore along the eastern coast of the island. These sediments have been precisely dated (Cornée et al., 2006; Titschack et al., 2013; Quillévéré et al., 2016) and contain abundant fossil fish otoliths that span a long time interval, from the Early to the Middle Pleistocene (Gelasian to Ionian). Fish otoliths are the aragonitic stone-like structure in the inner ear of Teleost fish that facilitate sound and balance perception (Schulz-Mirbach et al., 2018). They are considered an excellent tool for reconstructing past fish faunas due to their generally good preservation and abundance in marine and lake sediments (Nolf, 1985). In this study, we provide evidence for successive marine fish invasions and extripations in the marine fish fauna of the eastern Mediterranean during the Pleistocene. These events are correlated with the marine isotope stages (MIS) record of alternating glacial–interglacial cycles (Lisiecki and Raymo, 2005; Wang et al., 2010).

In the eastern Mediterranean, previous studies of the Pleistocene ichthyofauna have been conducted only in the Ionian Sea (Fig. 1; Girone, 2000; Girone and Varola, 2001; Sorbini and Landini, 2003; Landini and Sorbini, 2005a, 2005b; Girone et al., 2006a,b; Agiadi et al., 2010, 2011). As a result, the eastern Mediterranean fossil fish record remains poor. The examination of the Pleistocene fish otoliths of Rhodes comes to fill this knowledge gap. Furthermore, our synthesis of the marine fish record of the entire Mediterranean Sea, which has been derived from both skeletal and otolith material, from the Tortonian until today, leads to conclusions regarding the general trends in the marine fish faunas and their relation to climate and connectivity changes.

The gradually deteriorating climate and the oligotrophy of the Mediterranean Sea drove the general trends observed in the Pliocene–Pleistocene marine fish fauna. During the Pliocene, the Mediterranean was inhabited by tropical–subtropical fish of Atlantic or circumglobal distribution (Landini and Sorbini, 2005a; Agiadi et al., 2013). Invasions of cold-water Atlantic mesopelagic and bathypelagic fish have been recorded in the western Mediterranean since the Piacenzian and occurred throughout the Early Pleistocene, following the evolution of the Plio-Pleistocene Mediterranean paleoceanographic setting as well as the global climatic deterioration (Landini and Sorbini, 2005a; Girone et al., 2006a,b; Girone, 2007). During the Early and Middle Pleistocene, the climatic variability has been associated with changes in the relative contribution of cold- and warm-water mesopelagic fish species in the Ionian Sea assemblages (Agiadi et al., 2011). Mesopelagic subpolar–temperate species are found in this domain until the Late

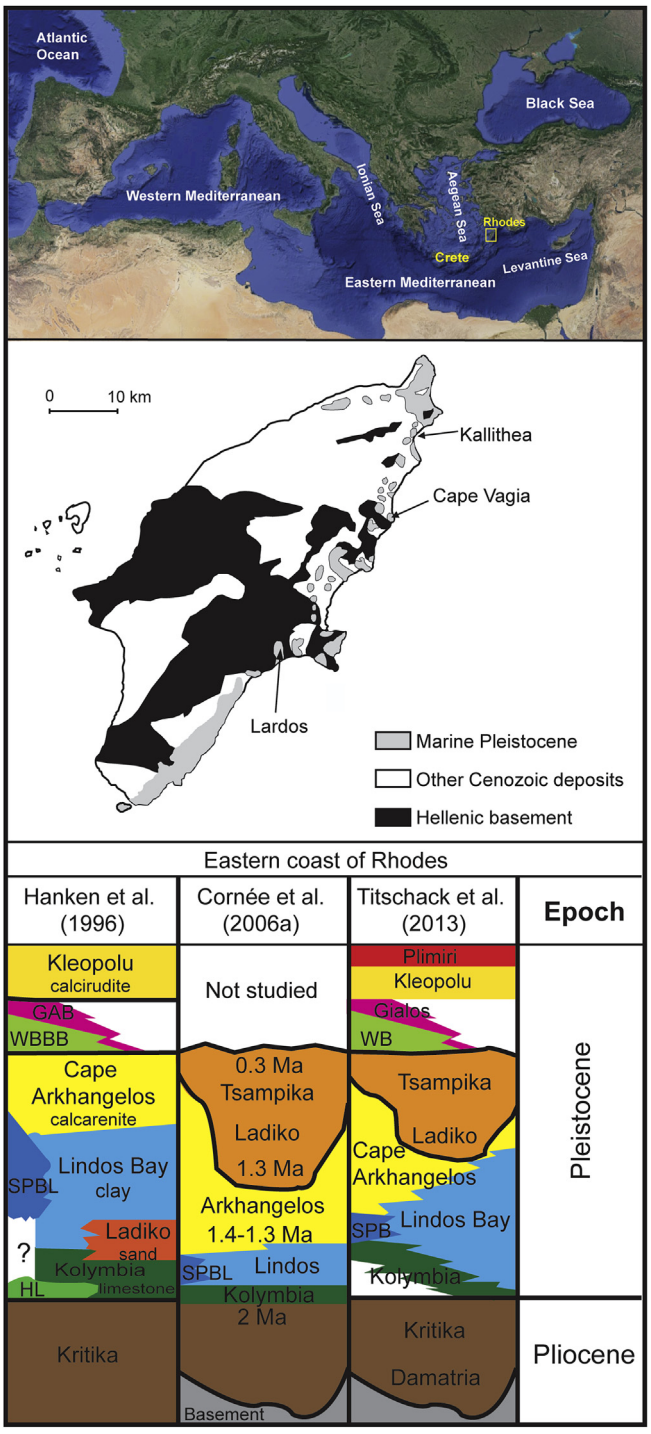

Fig. 1. Map of the Mediterranean Sea with the location of the island of Rhodes (upper panel). Simplified geological map of Rhodes showing the study areas (middle panel; modified from Mutti et al., 1970). Lithostratigraphic schemes for the Plio-Pleistocene deposits of the eastern coast of Rhodes HL: Haraki Limestone, SPBL: Saint Paul's Bay Limestone, WBBB: Windmill Bay Boulder Bed, GAB: Gialos Algal Biolithite, SPB: Saint Paul's Bay, WB: Windmill Bay (lower panel; modified from Quillévéré et al., 2016).

Pleistocene, and their occurrence has been attributed to climatic changes (Girone, 2003; Girone et al., 2006a,b).

The studied deposits of Rhodes correspond to a tectonically controlled transgressive–regressive cycle (Titschack et al., 2013; Quillévéré et al., 2016), which reached maximum paleodepths during the deposition of these otolith-rich clays (Hanken et al.,

1996; Cornée et al., 2006). Therefore, in addition, we estimate the paleodepth changes that occurred in these otolith-rich deposits using the identified fish assemblages, and evaluate our results in terms of the locally varying paleoenvironmental conditions, since depth is one of the most important parameters controlling fish distribution (Damalas et al., 2010; Rutterford et al., 2015).

2. Material and methods

2.1. Geological setting

The island of Rhodes is located in the easternmost part of the Hellenic forearc. It is influenced by intense tectonic activity and presents a great variety of environments today as well as in the past (Mutti et al., 1970; Moissette and Spjeldnaes, 1995; Hanken et al., 1996; Hansen, 1999; Cornée et al., 2006; Joannin et al., 2007). The geologic basement of Rhodes is built up by a series of stacked and folded tectonic units, including metamorphosed Mesozoic limestones as well as Cenozoic carbonate and siliciclastic deposits. During the Miocene, the southern and southwestern parts of Rhodes were emerged as a part of the Aegean land domain. The post-alpine sediments of Rhodes are separated into discrete lithostratigraphic units, as shown in Fig. 1, where the marine deposits recording the major Pleistocene transgressive–regressive cycle constitute the Rhodes Synthem (Cornée et al., 2006; Titschack et al., 2013; Quillévéré et al., 2016). Below the Rhodes Synthem, the Kritika Formation is composed of Gelasian brackish to shallow marine siliciclastic deposits (Moissette et al., 2016). The Rhodes Synthem comprises: the Kolymbia Formation at its base (late Gelasian to earliest Calabrian), with lower offshore bioclastic limestones, followed by the hemipelagic calcareous–silty clays of the Lindos Bay Formation that are the subject of this study (Calabrian to early part of the Ionian), and finally the Cape Arkhangelos Formation that reflects a major tectonic uplift of the island during the Middle Pleistocene (Quillévéré et al., 2016). Because of the intense tectonic activity affecting the island, the Pleistocene sediments are characterized by complex facies sequences, deposited within a series of paleovalleys along the northeastern coast of the island. We studied four sections originating from three different areas, along the eastern coast of Rhodes, from south to north: Lardos, Cape Vagia, and Kallithea (Fig. 1). These sections were chosen because: i) the outcrops are exposed well and allow extensive sampling, and ii) they have already been precisely dated (see below) and span the time interval from the late Gelasian to the Ionian.

2.2. Lithology, biostratigraphy, and sampling of the studied sections

2.2.1. Lardos section

A 30-m sequence of marine marls and sands crops out in the Lardos valley, a few kilometers east of Ypsenis Monastery (N 37°17′48″, E 27°8′4″; Figs. 1 and 2), corresponding to the upper part of the Lindos Bay Formation overlayed by littoral deposits of the Cape Archangelos Formation. Three samples (Lar1–3) were taken from the lower marl beds of the Lindos Bay Formation. On the eastern foothills, six samples (Lar4–9) were taken from a sandier, more littoral facies. Sample Lar5, in particular, was taken from a horizon showing the best macrofossil preservation, including many rhodoliths.

Titschack et al. (2013) provided an extensive investigation of this section based on calcareous nannoplankton, foraminifer assemblages, $\delta^{18}O$ of planktonic foraminifers, and $^{234}U/^{238}U$ dating of deep-sea corals (*Lophelia pertusa*). They assigned the deposition of the Lardos section to MIS 21–10 through correlation of the $\delta^{18}O$ curve with the corresponding oxygen isotope curve of ODP hole 967 (Kroon et al., 1998), providing an age between 0.9 and 0.3 Ma for these sediments (late Calabrian and Ionian). However, in the present study, sampling for otoliths was only possible in the intermediate part of the section, because the amount of sediment required for otolith study from the sand beds in the section would be too great to handle logistically, making sampling physically impossible. Through direct comparison with the section log provided by Titschack et al. (2013), the sampled interval is placed between 0.8 and 0.7 Ma and, therefore, falls in the late part of MIS20 up to the early part of MIS17 (Fig. 2).

2.2.2. Cape Vagia section

The Cape Vagia section (Fig. 1; N 36°14′98″, E 28°10′13″) was extensively studied by Løvlie et al. (1989), Moissette and Spjeldnaes (1995), Hanken et al. (1996), Kovacs and Spjeldnaes (1999), Steinthorsdottir et al. (2006), Cornée et al. (2006), and Quillévéré et al. (2016). The lower part of the sequence consists of 6 m limestones of the Kolymbia Formation, followed by 20 m marls of the Lindos Bay Formation, unconformably capped by a calcarenite corresponding to the Cape Arkhangelos Formation. One sample (Vag1) was taken from the Kolymbia Formation and seven samples (Vag2–8) from the Lindos Bay Formation (Fig. 2). Sample Vag3, in particular, was taken from laminated marls immediately following a red oxidized layer (Cornée et al., 2006) that was originally considered a volcanic tuff by Løvlie et al. (1989). Following Quillévéré et al. (2016), these collected samples are estimated to be late Gelasian to late Calabrian in age, between 2.0 Ma and 1.0 Ma (Fig. 2).

2.2.3. Kallithea sections

We studied two exposures in the Kallithea area, namely the Kallithea road section and the Kallithea beach section. The Kallithea road section is exposed along the coastal road north of Faliraki village (Fig. 1; N 36° 21′29.10″, E 28° 12′35.65″). The lower part of the section comprises ~20 m brackish sediments changing upward to transgressive littoral conglomerates of the Kritika Formation. Above, an atypical and mostly calcareous Kolymbia Formation sequence follows (Moissette et al., 2013), indicative of a deeper shelf edge depositional environment. These deposits are overlain by marls of the Lindos Bay Formation. The marls are unconformably covered by deposits belonging to uplifted Tarantian beaches. Five samples (Kal1–5) and two samples (Kal6–7) were taken from the Kolymbia Formation and the Lindos Bay Formation, respectively (Fig. 2).

The Kallithea road section was extensively studied by Thomsen et al. (2001) and Cornée et al. (2006). Two calcareous nannofossil bioevents were identified: the Last Occurrence (LO) of large *Gephyrocapsa* above sample-level Kal6 (1.617 Ma) and the LO of *Helicosphaera sellii* just below sample-level Kal7 (1.256 Ma). These observations, together with complementary biostratigraphic information based on foraminifers and ostracods, showed that the sediments sampled for the present study were deposited from the latest Gelasian to the Calabrian between 1.9 and 1.0 Ma.

The Kallithea beach section (Fig. 1; N 36° 37′ 83.84″, E 28° 23′ 81.70″) is located 8 km south of the city of Rhodes, on the coastal area of the homonymous thermae. Here, the post-alpine sequence encompasses 3 m marls corresponding to the uppermost part of the Lindos Bay Formation. These marls end in a conglomerate bed, followed by the Cape Arkhangelos Formation. Only the marls were sampled (Kal8), as it is not possible to extract any fish otoliths from the hardened calcarenite of the Cape Arkhangelos Formation. In this section, Nielsen and Hansen (2006) proposed a Pleistocene age for the upper part of Lindos Bay Formation, based on the occurrence of the pteropods *Cavolinia tridentata* and *Clio pyramidata*. Findings of the bivalve *Arctica islandica* in life position within the uppermost part of the overlying Cape Arkhangelos Formation denote an Ionian

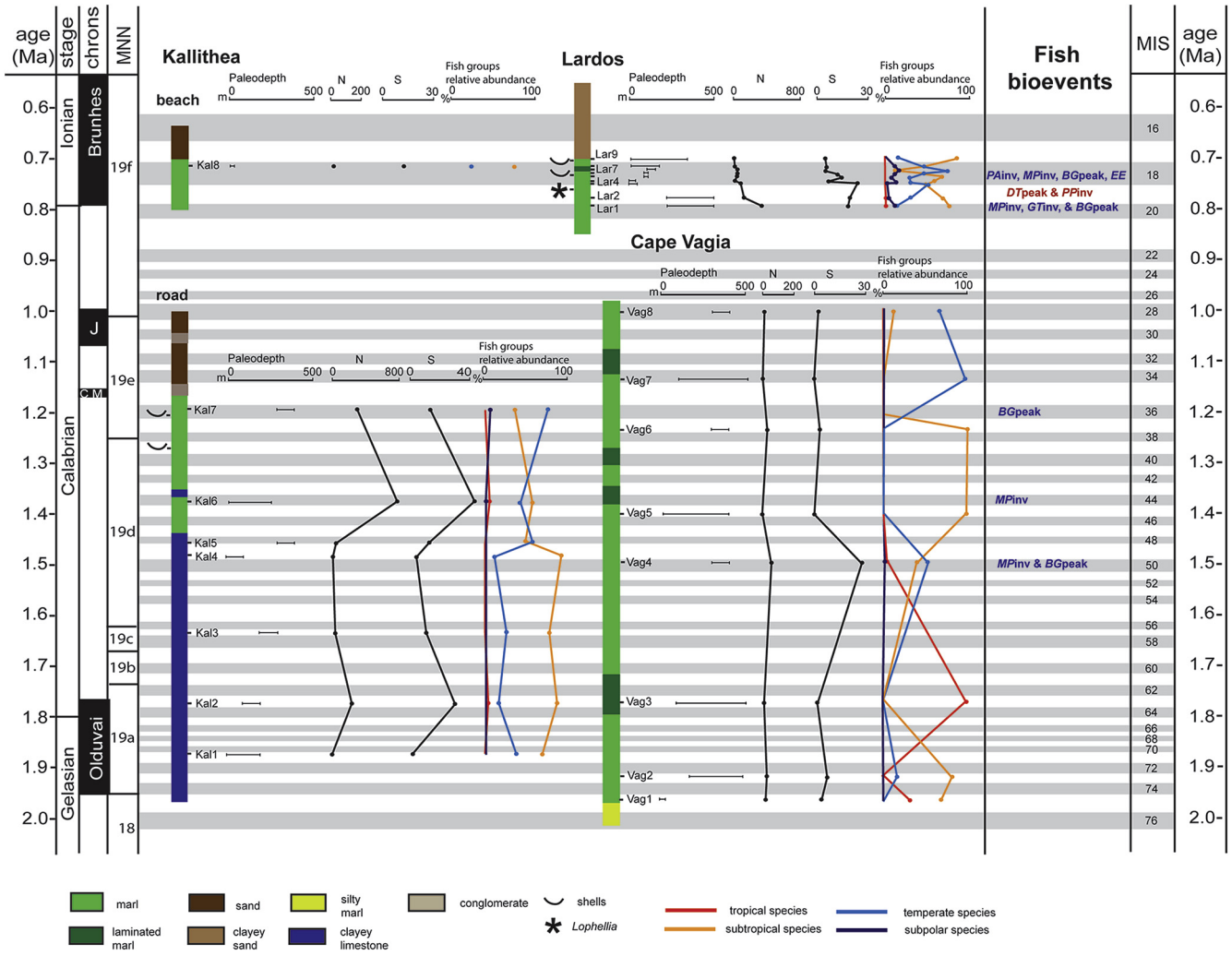

Fig. 2. Studied sections, sampling, paleobathymetry, fish fauna diversity (N: number of individuals, S: number of species), contribution of fish species according to their climatic affinity, and fish events in association with the marine isotope stages (MIS) of (Lisiecki and Raymo, 2005). Fish bioevents. *MP*inv: *Micromesistius poutassou* invasion, *GT*inv: *Gadiculus thori* invasion, *PA*inv: *Protomyctophum arcticum* invasion, *PP*inv: *Polyipnus polli* invasion, *BG*peak: peak in relative abundance of *Benthosema glaciale*, *DT*peak: peak in relative abundance of *Diaphus taaningi*, *EE*: establishment of *Engraulis encrasicolus*.

age for that part of the section. Two U/Th datings by Titschack et al. (2008) provided the ages of 108,600 yrs BP (+4,000, −3800) and 81,660 yrs BP (+4,510, −4340) for the upper part of Cape Arkhangelos Formation and the overlaying Windmill Bay Boulder Bed, respectively. Altogether, these data indicate that the upper part of Lindos Bay Formation sampled here in the Kallithea beach section was deposited during the early Ionian at ~0.8–0.7 Ma (Fig. 2).

2.3. Sample acquisition and processing

Approximately 25 kg of sediment were collected per sample along the studied sections (Fig. 2) in order to extract fish otoliths. The samples were diluted in plain water, sieved using a 250-μm diameter sieve, and dried. The otoliths were then handpicked from the residues under a stereomicroscope.

2.4. Otolith description and systematics

The otoliths were identified based on the morphologic characteristics described by Nolf (1985). New morphological observations are made on certain taxa and are presented here as supplementary material. The classification adopted is that of Nelson et al. (2016). Several taxa were left in open nomenclature due to insufficient knowledge of related Recent species or because the fossil material was too limited or too poorly preserved. Selected otoliths were photographed using a scanning electron microscope JEOL JSM-6360 at the Department of Historical Geology and Palaeontology of the University of Athens.

2.5. Paleoecological analyses

The identified fossil fish faunas were used to reconstruct the evolution of the paleoenvironments in the study areas. The assemblages were analyzed based on the modern distribution and ecological information about the fish species or their closest living relative, in case of extinct taxa (present-day ecological information is presented in supplementary Table S3). Depositional depths were estimated from the species present-day depth distributions (Froese and Pauly, 2018) and their otoliths as recorded in surficial sediments of the Mediterranean and the NE Atlantic (Lin et al., 2016, 2017b). Strongly eroded specimens were disregarded from this analysis, as they may have been transported to the depositional site. We compared the number of individuals (N) and the number of species (S) in the samples. Furthermore, we examined the

occurrences and relative abundances of the identified taxa considering their lifestyle; pelagic fishes (oceanic, epipelagic, mesopelagic, and bathypelagic depending on depth range) inhabit the water column, whereas benthic and bathypelagic (altogether demersal) fish occupy the sea bottom or are closely associated with it, respectively.

2.6. Paleobiogeographic analyses

The geographic distributions of the identified taxa were compared between the western and eastern Mediterranean during each chronostratigraphic unit from the Tortonian to the Late Pleistocene. In addition, these were compared to the present-day Mediterranean, Atlantic, and Indo-Pacific distributions of the taxa. Finally, the identified taxa were classified based on their modern climatic-zone affinity (Froese and Pauly, 2018), in order to examine the evolution of the entire ecosystem, in the eastern Mediterranean, in response to climate cycles during the Early and the Middle Pleistocene. The relative abundances of tropical, subtropical, temperate, and subpolar taxa were calculated for each 25-kg sample separately, following the methodology of Agiadi et al. (2011).

2.7. Taphonomic considerations

In the present analyses, certain taphonomic processes were identified that affected both the paleoecologic and the paleobiogeographic interpretations. First, we investigated transportation effects that have been reported in previous otolith studies (e.g., Agiadi et al., 2017), as well as in the overall fossil assemblages of the study area (Titschack et al., 2013). Moreover, we compared the paleoecologic and paleobiogeographic results between the studied sections, considering whether sampling resolution and/or local factors play a role in any differences between them. Finally, in order to explore the impact of taphonomic processes on the fossil fish record, the fish otolith and skeleton records in the south (Crete) and southeastern Aegean (Rhodes) were compared for the Pliocene and the Pleistocene.

3. Results and interpretation

In this section, the results are presented section-by-section, highlighting the most important findings and offering a paleoecologic interpretation and paleobathymetric estimations for the sampled sediments. The samples analyzed for the present study yield 67 species, belonging to 55 genera and 29 families (Table 1 and supplementary Tables S1 and S2; Figs. 3–5). Among these, 25 species (19 genera, 8 families) are pelagic, whereas the majority of the remaining 42 species (36 genera, 22 families) are benthic or benthopelagic fish.

3.1. Lardos area

At Lardos, the fish assemblages are dominated by myctophids in the lower part of the section, whose relative abundance decreases gradually toward the top, with increasing contribution of gadids, congrids, sparids, and gobiids (supplementary Tables S1 and S2). Notable are the occurrences of: a) *Engraulis encrasicolus* in samples Lar6 and Lar9, whose distribution in the present-day Mediterranean is controlled by shifts in areas of increased productivity (Piroddi et al., 2010; Bonanno et al., 2014); b) *Polyipnus polli* in sample Lar3, whose present-day relative abundance in the Atlantic Ocean is likely controlled by the absence of the cold and low-salinity Antarctic Intermediate Water (Olivar et al., 2017); c) cold-water *Gadiculus thori* in sample Lar1 (Gaemers and Poulsen, 2017); d) cold-water *Micromesistius poutassou* in samples Lar1, Lar3, and Lar7, whose relative abundance in the North Atlantic and the Mediterranean seems to be controlled by long-term temperature trends (Trenkel et al., 2015); and e) euryhaline *Atherina boyeri* in samples Lar5 and Lar8. Overall, the Lardos fish fauna is dominated by subtropical and temperate species, punctuated by increased abundances of cold-water species (Fig. 2). In particular, in addition to *Micromesistius poutassou*, we observe high abundances of the cold-water species *Benthosema glaciale* in samples Lar1, 2, 4, 6, and 8; and the presence of *Protomycrophum arcticum* in sample Lar5.

The occurrences of *Micromesistius poutassou* (sample Lar1) and *Gadiculus argenteus* (sample Lar2) indicate an upper continental slope depositional setting for the lower part of the Lardos section, since these species are typical of the upper continental slope and exhibit a maximum abundance between 200 and 400 m both in the Mediterranean and the Atlantic (supplementary Table S3). However, these taxa characterize fish otolith assemblages from Recent Mediterranean sediments between 300 and 500 m (Lin et al., 2017a, 2017b).

The benthic and benthopelagic components in sample Lar3 are a mixture of deep and shallow-water species. Gobiids and *Chromis chromis* dwell in shallow environments between 0 and 40 m, whereas gadids and *Polyipnus polli* originate from depths exceeding 250 m. This therefore suggests that this mixing occurred in a slope environment with rapidly changing paleodepths.

Upward in the section, the benthic-benthopelagic component is enriched with shallow-water taxa such as *Chromis chromis* and *Oblada melanura*, whose depth distributions do not exceed 30 m (sample Lar4). The otolith associations are also characterized by greater abundances and diversity of gobiids such as *Aphia minuta* and *Deltentosteus quadrimaculatus*, which are found in depths less than 100 m.

In sample Lar6, we find the anchovy *Engraulis encrasicolus* and the very shallow goby *Pomatoschistus* sp. together with *G. argenteus*. In sample Lar7, *G. argenteus* and *M. poutassou* are associated with *A. minuta* and in sample Lar9, the gadid is associated with *Atherina boyeri*, whose depth range does not usually exceed 5 m. Hence, we propose that the study area was a steep coastal environment with easy access to the open ocean.

3.2. Vagia area

The pelagic assemblages at Vagia exhibit important changes in diversity. Samples Vag1, Vag3, and Vag5 lack taxa occupying the upper part of the water column. Sample Vag2 exhibits a strong subtropical component, composed of mesopelagic myctophid species. Sample Vag4 exhibits the most diversified assemblage dominated by temperate species; the presence of *Engraulis encrasicolus* and *Electrona risso* is particularly significant, indicating increased productivity, which would favor the development of a small pelagic fish spawning site in this area (Piroddi et al., 2010; Bonanno et al., 2014). However, the upper part of the section (samples Vag6, Vag7, and Vag8) contains a very poor pelagic assemblage, comprised only of myctophids and *Cepola macrophthalma*.

A paleodepth of 0–15 m is estimated for sample Vag1 based on the co-occurrence of *Gobius paganellus, Pomatoschistus* sp., and *Carapus acus*. *Carapus acus* is found up to 150 m depth today (Nielsen et al., 1999), *Gobius paganellus* occupies depths up to 15 m (Azevedo and Simas, 2000), and *Pomatoschistus* spp. are found in shallow waters as well. Sample Vag2 exhibits a higher mesopelagic component and was deposited deeper due to the high abundance of myctophids, especially *Diaphus taaningi*, whose depth range is 40–475 m (Quéro et al., 1990), and the presence of *Ophidion*

Table 1
Geographic and stratigraphic distribution of the identified fish taxa. The respective outcrops, where the identified material has been found, are indicated in the column "studied material"; La: Lardos, Va: Vagia, Ka: Kallithea. Present-day distributions are according to the Fishbase database (Froese and Pauly, 2018). Dark grey: taxa whose record in the present study is the first in the eastern Mediterranean Sea for the interval noted. Light grey: taxa reported in the eastern Mediterranean before, but only in the Ionian realm. Present-day Indo-Pacific distribution of *Maurolicus muelleri* is confined to the eastern part of the Pacific Ocean. Also, at present, *Grammonus ater* may be found in the Mediterranean, from the western sub-basin to the Adriatic Sea. References: 1. Agiadi et al. (2011), 2. Landini and Sorbini (1993), 3. Nolf and Girone (2006), 4. Brzobohaty and Norf (2000), 5. Brzobohaty and Nolf (1996), 6. Nolf and Martinell (1980), 7. Nolf et al. (1998), 8. Girone (2007), 9. Nolf and Cappetta (1988), 10. Carnevale et al. (2006), 11. Markopoulou-Diakantoni and Kagiouzis (2001), 12. Gaudant (2002), 13. Landini and Sorbini (2005b), 14. Nolf and Cavallo (1995), 15. Schwarzhans (1979), 16. Anfossi et al. (1982), 17. Anfossi and Mosna (1979), 18. Landini et al. (1990), 19. Gaudant (2001), 20. Gaudant et al. (1994), 21. Sorbini (1988), 22. Landini and Menesini (1986), 23. Landini and Menesini (1978), 24. Sorbini and Landini (2003), 25. Landini and Varola (1983), 26. Girone (2000), 27. Girone and Varola (2001), 28. Girone (2003), 29. Anfossi and Mosna (1972), 30. Aruta and Greco (1980), 31. Bossio et al. (1986), 32. Nolf and Girone (2000), 33. Anfossi and Mosna (1976), 34. Girone et al. (2010), 35. Schwarzhans (1999), 36. Girone et al., 2006a,b, 37. Agiadi et al. (2013), 38. Agiadi et al. (2017), 39. Karakitsios et al. (2017), 40. Moissette et al. (2018).

Family	Taxon	western Mediterranean									eastern Mediterranean											Studied material	References
		Miocene		Pliocene		Pleistocene					Miocene		Pliocene		Pleistocene								
		Tortonian	Messinian	Zanclean	Piacenzian	Gelasian	Calabrian	Middle	Late	Holocene	Tortonian	Messinian	Zanclean	Piacenzian	Gelasian	Calabrian	Ionian	Late	Holocene	Present-day Atlantic	Present-day Indo-Pacific		
PELAGIC TAXA																							
Engraulidae	*Engraulis encrasicolus*				+	+	+	+		+						+	+		+	+		La, Va, Ka	36
Clupeidae	*Sardinella maderensis*			+						+						+			+	+		Va	3,7
Gonostomatidae	*Gonostoma* sp.	+	+	+			+	+		+						+	+		+	+	+	La	36
Sternoptychidae	*Maurolicus muelleri*	+	+	+	+	+	+	+		+	+	+	+	+	+	+	+		+	+	+	La, Ka, Va	1,2,3,8,9,12,13,14,16,18,19,21,22,23,24,25,26,27,28,34,37
Phosichthyidae	*Vinciguerria* cf. *attenuata*						+	+		+							+		+	+	+	La	36
	Vinciguerria poweriae	+	+	+	+	+	+	+		+			+	+	+	+	+		+	+	+	Ka, Va	1,3,8,9,13, 22, 24,25,26,28,36,37
Scopelarchidae	*Scopelarchus analis*	+	+	+		+	+	+							+	+				+	+	Va	34,36
Myctophidae	*Benthosema glaciale*		?	+	+	+	+	+	+	+		?	+	+	+	+	+		+	+		La, Ka, Va	36
	Benthosema suborbitale			+	+	+	+									+	+			+	+	La	36
	Ceratoscopelus maderensis			+	+	+	+	+		+			+	+	+	+	+		+	+		La, Va, Ka	1,3,5,6,7,8,9,11,12,13,14,15,21,22,24,25,26,27,28,29,30,31,32,37
	Diaphus holti	+	+	+	+	+	+			+			+	+	+	+	+		+	+	+	La, Va, Ka	1,3,4,6,7,9,13,22,23,26,28,33, 36,37
	Diaphus rafinesquii	+	+	+	+	+	+			+		+	+	+	+	+	+		+	+		La, Va, Ka	1,3,4,6,8,9,13,14,23,26,27,28,29,31,34,36,37
	Diaphus taaningi	+	+	+	+	+	+	+				+	+	+	+	+	+			+	+	La, Va, Ka	1,4,7,9,13,26,27,28,34,37
	Electrona risso			+	+	+	+	+	+	+			+	+	+	+	+		+	+	+	Ka, Va	36
	Hygophum benoiti					+				+			+	+	+	+	+		+	+		La, Va, Ka	1,8,13,23,24,26,27,28,37
	Hygophum hygomii	+	+	+	+	+	+	+		+		+	+	+	+	+	+		+	+	+	La, Ka	1,3,5,6,7,8,9,13,14,15,22,23,24,26,27,28,29,31,32,34,37
	Lampadena sp.	+		+	+	+	+	+		+			+	+	+	+						Ka	34,36
	Lampanyctus crocodilus					+	+	+		+					+	+	+		+	+		Ka, Va	36
	Lobianchia dofleini	+	+	+	+	+	+			+		+	+	+	+	+	+		+	+	+	La, Va, Ka	1,5,7,9,7,13,14,22,23,25,26,27,28,31,34,37
	Myctophum punctatum			+	+	+	+	+		+				+	+	+	+		+	+		La, Va, Ka	36
	Notoscopelus elongatus	+				+	+	+		+	+				+	+	+		+	+		La, Va, Ka	36, 38
	Protomyctophum arcticum								+								+			+		La	36
	Scopelopsis pliocenicus	+		+	+		+						+	+	+	+	+					La, Ka	1,3,5,6,7,8,9,13,15,26,28,29,33,34,37
Gobiidae	*Aphia minuta*		+				+	+		+			+		+	+	+		+	+		La, Va, Ka	13,27,34,37

Family	Taxon	western Mediterranean									eastern Mediterranean									Present-day Atlantic	Present-day Indo-Pacific	Studied material	References
		Miocene		Pliocene		Pleistocene					Miocene		Pliocene		Pleistocene								
		Tortonian	Messinian	Zanclean	Piacenzian	Gelasian	Calabrian	Middle	Late	Holocene	Tortonian	Messinian	Zanclean	Piacenzian	Gelasian	Calabrian	Ionian	Late	Holocene				
BENTHIC AND BENTHOPELAGIC TAXA																							
Congridae	*Conger conger*	?	?	+	+	+	+	+		+	?	?	+	+		+	+		+	+		La, Ka	27,32
	Gnathophis mystax			+						+							+		+	+		La	3
	Pseudophichthys splendens	+	+	+	+							+	+			+				+		Ka, Va	3,8,34,37
Argentinidae	*Argentina sphyraena*		+	+	+		+	+		+		+	+	+		+	+		+	+		La	34,36
Sternoptychidae	*Polyipnus polli*															+	+			+		La, Ka	27
Chlorophthalmidae	*Chlorophthalmus agassizi*									+			+			+	+		+	+	+	Ka	1,37
Moridae	*Laemonema* sp.	+			+		+	+			+		+	+	+	+				+	+	Ka	1,8,34,36,37
Carangidae	*Trachurus* sp.	+	+		+	+	+	+		+				+	+	+	+		+	+	+	La, Ka	27,36
Centracanthidae	*Spicara smaris*			+	+	+	+	+		+			+	+	+	+	+		+	+		La, Ka	28,36
Macrouridae	*Coelorinchus* sp.	+		+		+	+			+	+		+		+	+	+		+	+		La	34
Phycidae	*Gaidropsarus* sp.					+	+	+		+					+	+	+		+	+		La, Va, Ka	27,36
	Phycis blennoides	+			+	+	+	+		+					+	+	+	+				La	36
Gadidae	*Gadiculus argenteus*	+	+	+	+	+	+	+		+	?	+	+	+	+	+	+		+	+		La, Va, Ka	34,36
	Gadiculus labiatus	+	+	+	+	+	+				+	+	+	+	+	+						Va	1,2,3,6,7,8,9,13,14, 16,17,19,21,29,34, 36,37
	Gadiculus thori					+	+	+							+		+			+		La	36
	Micromesistius poutassou			+	+	+	+	+		+			+	+	+	+	+		+	+		La, Va, Ka	36
Ophidiidae	*Ophidion barbatum*			+	+	+	+	+		+						+	+		+	+		Ka	27,36
	Monomitopus metriostoma															+	+			+		Va, Ka	
Bythitidae	*Grammonus ater*							+		+			+		+	+	+		+	+		La, Va, Ka	27,36,37
Carapidae	*Carapus acus*			+	+	+	+	+		+						+	+		+	+		Ka, Va	36
	Echiodon dentatus			+						+			+			+	+		+	+		Ka	13,27,32,36,37
Atherinidae	*Atherina boyeri*		+				+			+		+	+			+	+		+	+		La, Va, Ka	12,34,36,37
Scorpaenidae	*Scorpaena* sp.			+						+						+	+		+	+		La	7
Acropomatidae	*Verilus mutinensis*	+	+	+	+	+	+				+	+	+	+	+	+						Va	1,3,6,7,8,9,13,14,15 16,17,29,33,34,36
Sparidae	*Dentex* spp.	+	+	+	+	+	+	+		+	+	+	+	+	+	+	+		+	+		La, Va, Ka	27,36
	Diplodus cf. *annularis*									+						+			+	+		Ka	
	Oblada melanura			+						+			+			+	+		+	+		La, Va	3,37
	Pagellus cf. *bogaraveo*									+						+			+	+		Ka	
	Pagrus pagrus				+					+						+			+	+		Ka	
Cepolidae	*Cepola macrophthalma*	+	+	+	+	+	+	+		+	+	+	+	+	+	+	+		+	+		La, Va, Ka	3,6,7,8,9,13,14,17, 18,26,27,29,32,33, 34,35,37
Pomacentridae	*Chromis chromis*							+		+						+	+		+	+		La, Ka	
Blennidae	*Blennius ocellaris*						+	+		+						+	+		+	+		La	27,36
Gobiidae	*Chromogobius zebratus*															+	+		+			La, Ka	
	Deltentosteus quadrimaculatus			+	+	+	+	+		+			+	+	+	+	+		+	+		La, Va, Ka	1,3,13,26,27,32
	Gobius niger		+	+	+	+	+	+		+			+	+	+	+	+		+	+		La, Ka	3,10,13,18, 32,37
	Gobius cf. *paganellus*									+			+			+			+	+		La, Va, Ka	37
	Lesueurigobius friesii			+	+					+	+	+	+		+	+	+		+	+		Ka, Va	3,8,17,26,27,32,37, 40
	Lesueurigobius sanzi		+	+						+		+	+			+				+		Ka	3,7,34,37
	Lesueurigobius suerii			+	+	+	+	+		+	+	+	+	+	+	+	+		+	+		La, Va, Ka	3,14,27,32, 37,40
Bothidae	*Arnoglossus kokeni*	+		+	+		+				+		+	+	+	+						Va	3,6,9,13,14,17, 26,27,32,34,35

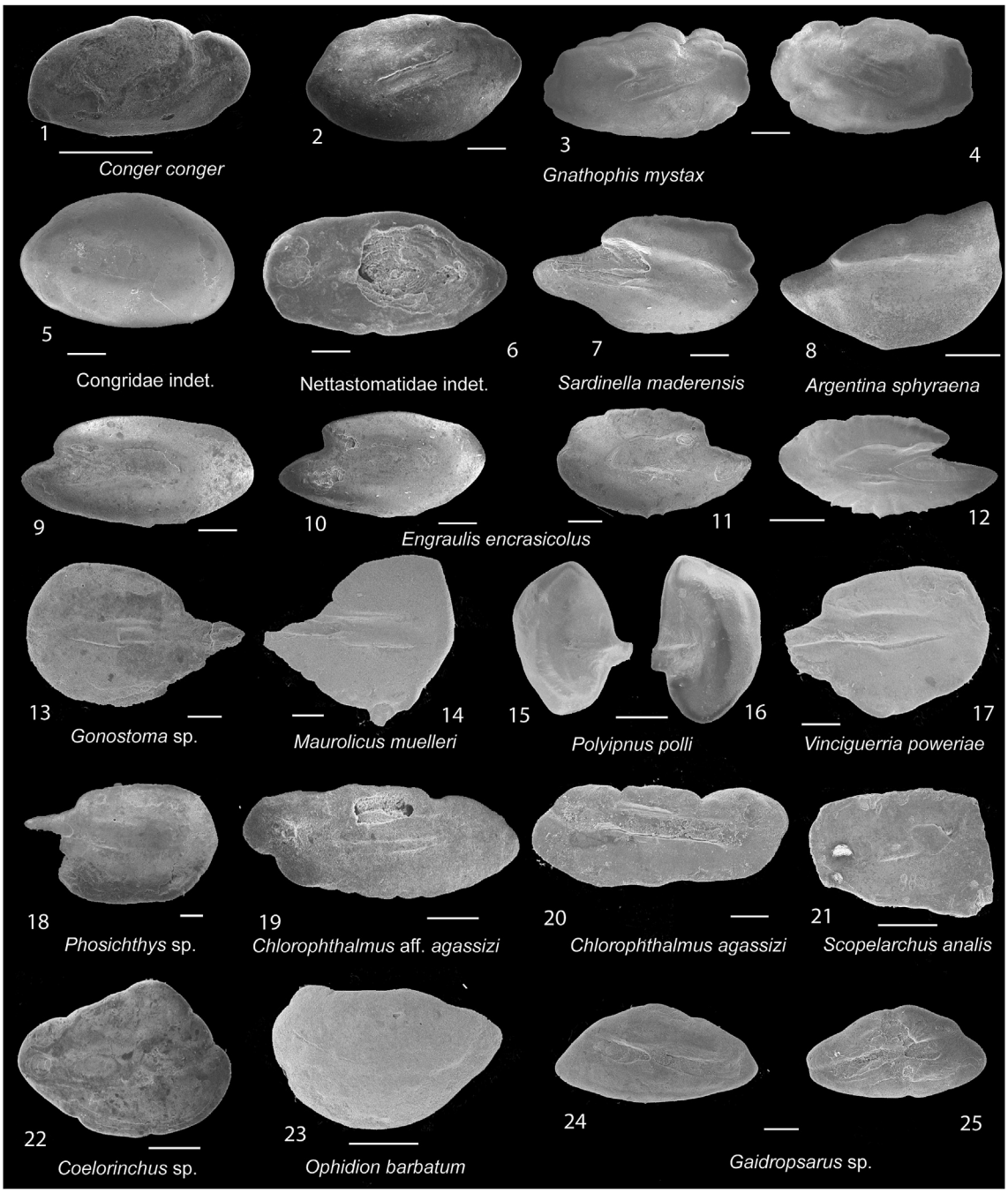

Fig. 3. Photographs of the identified and comparative material. Congridae: 1. *Conger conger* (Linnaeus, 1758) Lar5; 2. *Gnathophis mystax* (Delaroche, 1809) Lar3; 3–4. *Gnathophis mystax* (Delaroche, 1809) Lar3; 5. indet. Vag4. Nettastomatidae: 6. indet. Vag4. Clupeidae: 7. *Sardinella maderensis* (Lowe, 1838) Vag4. Argentinidae: 8. *Argentina sphyraena* Linnaeus, 1758, Lar6. Engraulidae: 9–12. *Engraulis encrasicolus* (Linnaeus, 1758) 9–10. Lar6; 11. Vag4; 12. Kal8. Gonostomatidae: 13. *Gonostoma* sp. Lar2. Sternoptychidae: 14. *Maurolicus muelleri* (Gmelin, 1789) Vag4; 15–16. *Polyipnus polli* Schultz, 1961, Lar3. Phosichthyidae: 17. *Vinciguerria poweriae* (Cocco, 1838) Vag4; 18. *Phosichthys* sp. Lar2. Chlorophthalmidae: 19. *Chlorophthalmus* aff. *agassizi* Bonaparte, 1840, Kal6; 20. *Chlorophthalmus agassizi* Bonaparte, 1840, recent from the eastern Ionian Sea. Scopelarchidae: 21. *Scopelarchus analis* (Brauer, 1902) Vag4. Macrouridae: 22. *Coelorinchus* sp. Lar2. Ophidiidae: 23. *Ophidion barbatum* Linnaeus, 1758, Kal6. Lotidae: 24–25. *Gaidropsarus* sp. Vag4. Scale: 100 μm for photographs 5, 7, 11, and 18; 200 μm for photographs 6, 9–10, 13–14, 17, and 24–25; 500 μm for photographs 1–4, 12, 15–16, 19–20, and 22; and 1 mm for photographs 8, 21, and 23.

barbatum, whose modern depth range exceeds 150 m (Goren and Galil, 2015). Thus, the paleodepth for this level is estimated at 150–475 m. Sample Vag3 contains only specimens of the extinct species *G. labiatus*, known from the Miocene up to the middle Pliocene and from a wide range of environments. Based on the present-day distribution of *Gadiculus* spp., we can infer that this species also occupied depths greater than 100 m.

The topography may again be implicated for the apparently mixed fish assemblage found in sample Vag4. The shallow-water group, between 0 and 30 m, comprises *Sardinella maderensis*, *Oblada melanura,* and several gobiids. In the same level, however, there are several gadids. Overall, the most abundant species in the assemblage at this level are *Maurolicus muelleri*, *Ceratoscopelus maderensis*, and *Gadiculus argenteus*. Based on the composition of the death assemblages in surficial sediments of the Mediterranean (Lin et al., 2017b), this association indicates a depositional depth of

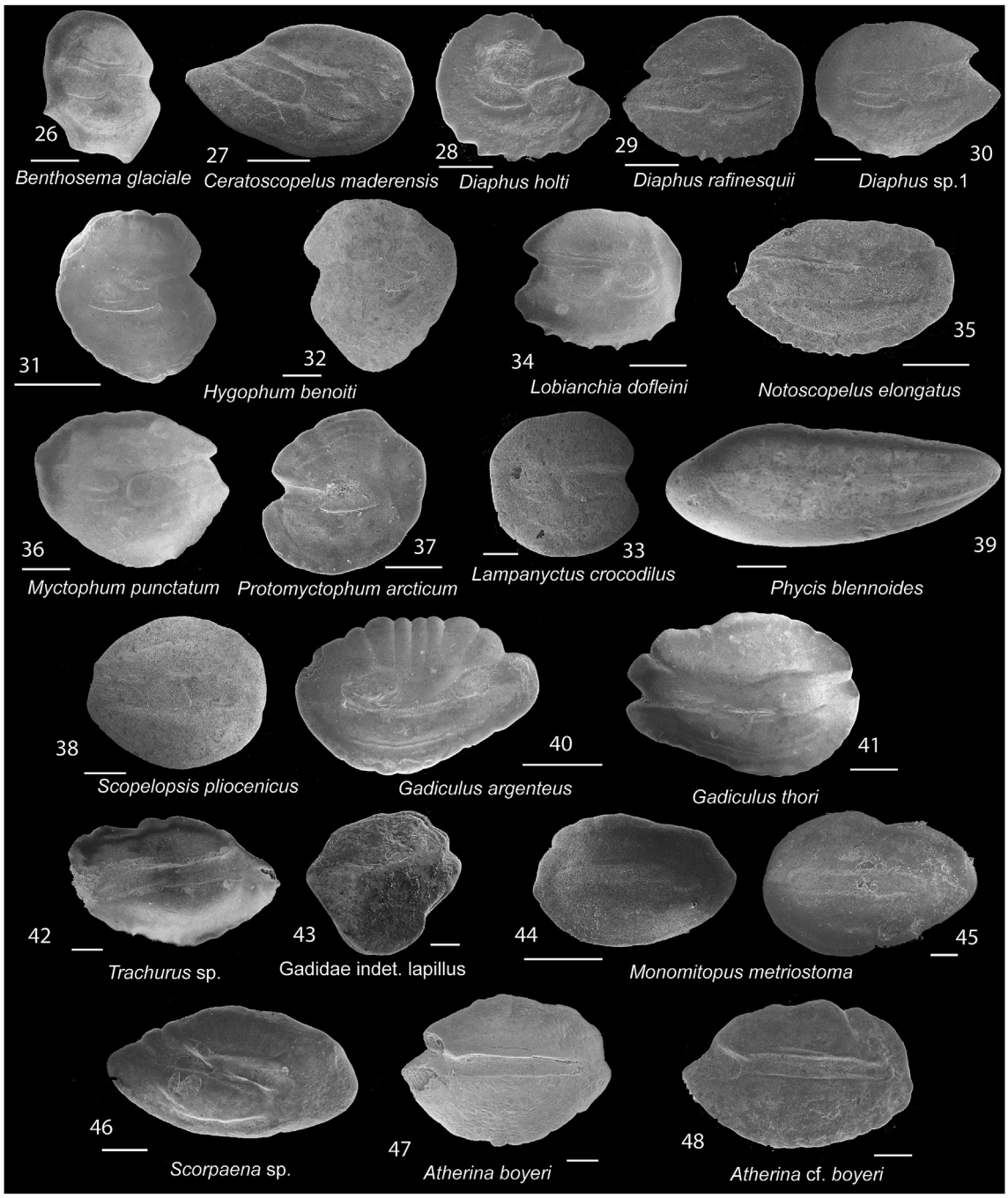

Fig. 4. Photographs of the identified and comparative material (continuation). Myctophidae: 26. *Benthosema glaciale* (Reinhardt, 1837) Lar1; 27. *Ceratoscopelus maderensis* (Lowe, 1839) Lar1; 28. *Diaphus holti* Taaning, 1918, Lar3; 29. *Diaphus rafinesquii* (Cocco, 1838) Lar2; 30. *Diaphus* sp.1, Lar1; 31–32. *Hygophum benoiti* (Cocco, 1838), 31. Vag4; 32. Lar3; 33. *Lampanyctus crocodilus* (Risso, 1810) Lar2; 34. *Lobianchia dofleini* (Zugmayer, 1911) Lar2; 35. *Notoscopelus elongatus* (Costa, 1844) Lar3; 36. *Myctophum punctatum* (Rafinesque, 1810) Lar1; 37. *Protomyctophum arcticum* (Lütken, 1892) Lar5; 38. *Scopelopsis pliocenicus* (Anfossi and Mosna, 1976) Lar2. Phycidae: 39. *Phycis blennoides* (Brünnich, 1768) Lar3. Gadidae: 40. *Gadiculus argenteus* Guichenot, 1850, Lar6, 41. *Gadiculus thori* Schmidt, 1913, Lar1. Carangidae:42. *Trachurus* sp. Lar5. Gadidae: 43. Gadidae indet. lapillus, Lar2. Ophidiidae: 44–45. *Monomitopus metriostoma* (Vaillant, 1888) 44. Vag2; 45. Vag4. Scorpaenidae: 46. *Scorpaena* sp. Lar3. Atherinidae: 47. *Atherina boyeri* Risso, 1810, Vag4, 48. *Atherina* cf. *boyeri* Risso, 1810, Lar5. Scale: 100 μm for photograph 45; 200 μm for photographs 32, 42, 43, and 47; 500 μm for photographs 26–28, 30–31, 34–39, 44, 46, and 48; and 1 mm for photographs 29 and 40–41.

300–400 m for this interval. Sample Vag5 contains only *Lesueurigobius friesii*, which is abundant in surficial sediments of the Mediterranean between 300 and 400 m (Lin et al., 2017b), even though its present-day depth range is 10–130 m (supplementary Table S3); nevertheless, we cannot give a precise paleodepth estimate based only on one species. *Cepola macrophthalma*, *Diaphus rafinesquii*, and *Notoscopelus elongatus* in samples Vag6 and Vag8 suggest a depth between 300 and 400 m, based on their natural depth distributions (Quéro et al., 1990) and their abundance in surficial sediments of the Mediterranean (Lin et al., 2017b). Finally, sample Vag7 only contains *Ceratoscopelus maderensis* and its paleodepth estimate consequently remains very broad.

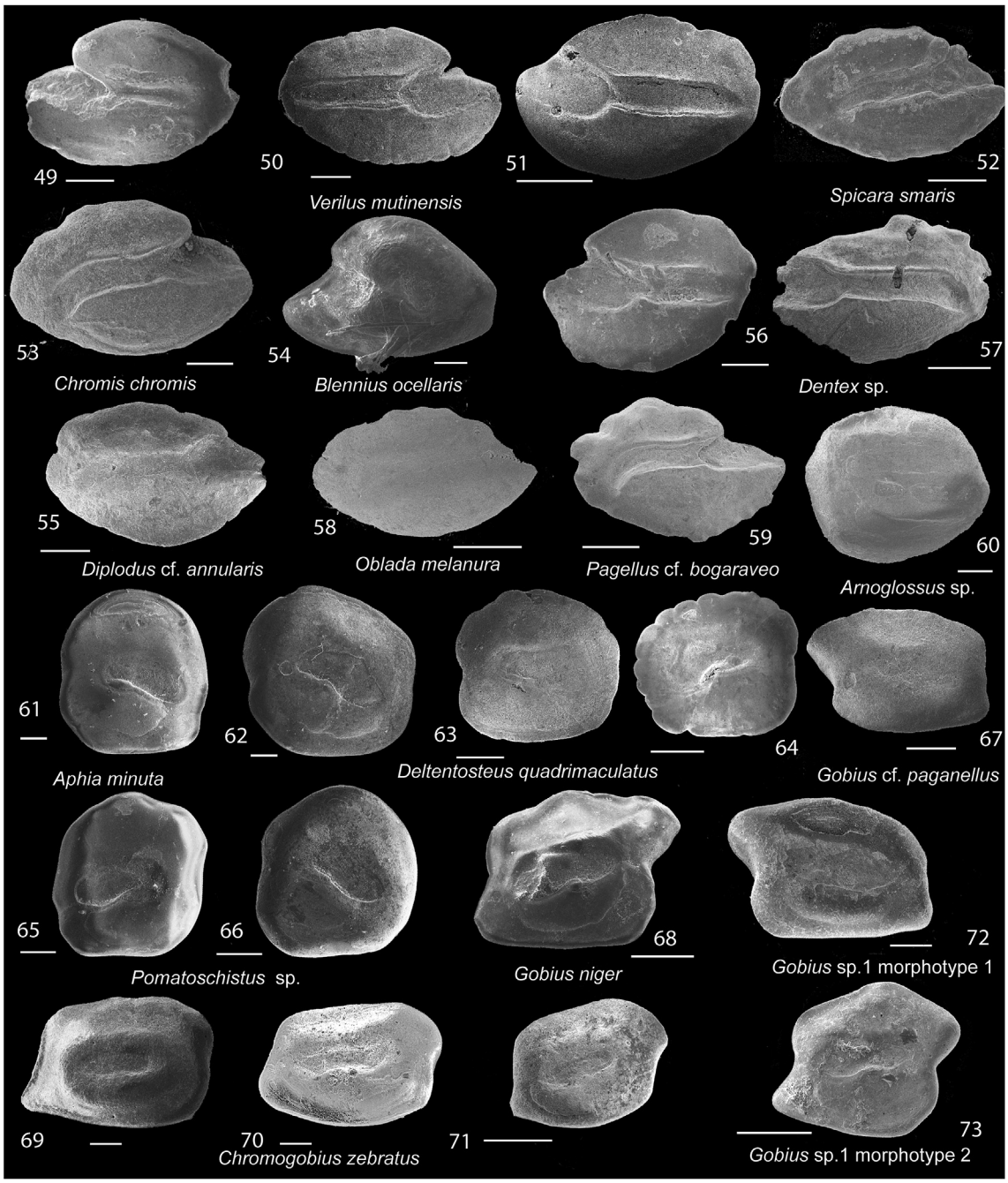

Fig. 5. Photographs of the identified and comparative material (continuation). Acropomatidae: 49–51. *Verilus mutinensis* (Bassoli, 1906) 49. Vag4; 50–51. Paliore river (Di Geronimo et al., 2003). Centracanthidae: 52. *Spicara smaris* (Linnaeus, 1758) Lar5. Pomacentridae: 53. *Chromis chromis* (Linnaeus, 1758) Lar3. Blennidae: 54. *Blennius ocellaris* Linnaeus, 1758, Lar9. Sparidae: 55. *Diplodus* cf. *annularis* (Linnaeus, 1758) Kal6; 56–57. *Dentex* sp., 56. Vag4; 57. Lar3; 58. *Oblada melanura* (Linnaeus, 1758) Vag4; 59. *Pagellus* cf. *bogaraveo* (Brünnich, 1768) Kal6. Bothidae: 60. *Arnoglossus* sp. Vag4. Gobiidae: 61. *Aphia minuta* (Risso, 1810) Lar4; 62–64. *Deltentosteus quadrimaculatus* (Valenciennes, 1837) 62. Lar5; 63. Vag4, 64. Kal2; 65–66. *Pomatoschistus* sp., Lar6; 67. *Gobius* cf. *paganellus* Linnaeus, 1758, Kal6; 68. *Gobius niger* Linnaeus, 1758, Lar3; 69–71. *Chromogobius zebratus*, 69. Lar6; 70–71. Kal2. 72. *Gobius* sp.1 morphotype 1, Lar5; 73. *Gobius* sp.1 morphotype 2, Lar5. Scale: 200 μm for photographs 49, 54, 60–62, 65–66, and 69–70; and 500 μm for photographs 50, 52–53, 55–56, 58–59, 63–64, 67–68, and 71–73.

3.3. Kallithea area

At Kallithea, the fish assemblages are characterized by high diversity in both pelagic and benthic-benthopelagic components. Subtropical fish assemblages dominate the Calabrian deposits of the Kallithea road section (Fig. 2). Nevertheless, we note that the relative contributions of the species *M. poutassou* and *B. glaciale* increase in the upper part of the section in samples Kal6 and Kal7. Today, both species inhabit the north subpolar region and are therefore considered cold-water species. Moreover, there is a great increase in the assemblage size (number of individuals) and diversity (number of species) in samples Kal2 and Kal6. The fish fauna found there appears to be mainly subtropical, with a significant temperate component. The pelagic assemblage mostly comprises mesopelagic myctophids and *E. encrasicolus*, while the benthic-benthopelagic domain is inhabited by *Atherina boyeri*, *Cepola*

macrophthalma, and several gobiid species.

In the lower part of the Kallithea road section (Kal1), the assemblage shows low diversity. However, we note the high abundance of the benthic species *Lesueurigobius suerii*, which is more abundant in surficial sediments deposited at shallow depths up to 100 m (Lin et al., 2017b), although its living depth today reaches 377 m in the Ionian Sea (Mytilineou et al., 2005). However, this species is accompanied by *Ceratoscopelus maderensis*, which exhibits a great depth distribution in the eastern Mediterranean (Goren and Galil, 2015) and is found most abundant between 100 and 200 m in surficial sediments of the Mediterranean (Lin et al., 2016, 2017b). In addition, we find a high abundance of *Gobius* sp. specimens in the same sample, also indicating shallow depths. Therefore, we estimate the paleodepth for this level at 0–200 m.

In sample Kal2, the great abundance of shallow-water species such as *Chromis chromis*, *Oblada melanura, Diplodus annularis,* and gobiids suggests a shelf environment with depth probably below 100 m, but not exceeding 200 m. The occurrences of the gobiids *G. niger* and *L. friesii,* as well as *Monomitopus metriostoma* in sample Kal3 indicate depths between 200 and 300 m based on their abundance by depth in surficial sediments (Lin et al., 2017b), although these species live at shallower depths (supplementary Table S3). On the other hand, the concurrent occurrences of *D. quadrimaculatus* and juvenile specimens of *L. crocodilus* in sample Kal4 indicate a paleodepth less than 100 m for this level. Sample Kal5 contains specimens of both *G. niger* and *G. argenteus* indicating a paleodepth between 300 and 400 m. In sample Kal6, the taphocoenosis may be split into three groups. Group *A* comprises shallow water benthic-benthopelagic taxa, namely *Ophidion barbatus, Diplodus annularis, Chromis chromis, Gobius niger, Gobius paganellus,* and *Lesueurigobius friesii*. Group *B* consists of *Pseudophichthys splendens, Polyipnus polli, Vinciguerria poweriae, Laemonema* sp., *Chlorophthalmus agassizi*, and the gadids *Gadiculus argenteus* and *Micromesistius poutassou*, which may be found in deeper water levels. Few taxa occur in both shelf and upper slope settings, such as *Lampanyctus crocodilus, Gaidropsarus* sp., *Pagellus bogaraveo, Spicara smaris, Cepola macrophthalma, Deltentosteus quadrimaculatus,* and *Lesueurigobius suerii*, and are placed under Group *C*. Consequently, the paleodepth is estimated between 0 and 250 m. The observed mixing of the assemblages is yet again an indication of a high bathymetric gradient that characterized this area. Finally, sample Kal7 contains again gobiids, myctophids, and *Gadiculus argenteus*, suggesting a depth between 300 and 400 m.

In the Kallithea beach section (Kal8), the presence of *Gobius* cf. *paganellus* indicates that deposition took place at very shallow depths, between 0 and 15 m.

4. Discussion

4.1. Mediterranean teleost fish paleobiogeographic distribution

The stratigraphic and geographic distributions of the identified taxa are presented in Table 1. Overall, the stratigraphic distribution of 63 taxa is significantly extended. In particular, 24 species are reported for the first time in the Calabrian of the eastern Mediterranean, and the Ionian stage record is enriched by 15 taxa.

The pelagic fish, oceanic and epipelagic, include members of the families Engraulidae, Gonostomatidae, Sternoptychidae, Phosichthyidae, Clupeidae, Scopelarchidae; Myctophids however are by far the most diverse and abundant family. *Scopelarchus analis* can safely be assumed to have inhabited the Mediterranean Sea until the Calabrian. In addition, *Scopelopsis pliocenicus* may be found until the Ionian. Importantly, the arctic mesopelagic species *Protomyctophum arcticum* is reported here for the first time in Ionian deposits of the eastern Mediterranean. Girone et al., 2006a,b previously reported *P. arcticum* only from the Late Pleistocene of the western Mediterranean.

The most abundant and diverse benthic-benthopelagic groups are congrids, gadids, sparids and gobiids. Five congrid species have inhabited the eastern Mediterranean from the Early Pliocene to the Recent. *Conger conger* appears present the entire time, until today. *Gnathophis mystax* is here reported for the first time in the Calabrian. Previously, it was reported from the western Mediterranean only, in Tortonian (Lin et al., 2017a) and Zanclean deposits of Northern Italy (Nolf and Girone, 2006). *Pseudophichthys escavaratierensis*, previously identified in the late Zanclean of Crete (Agiadi et al., 2013), shows no record in the Pleistocene sediments studied here.

Furthermore, the Atlantic species *Polyipnus polli*, absent today from the eastern Mediterranean realm, is identified here for the first time in the Calabrian. This species has previously been found in Ionian sediments of Montalbano Jonico in Italy (Girone and Varola, 2001). Furthermore, the genus *Polyipnus* seems to have migrated in the western basin from the Piacenzian (Girone, 2007). The presently abundant deep-water *Chlorophthalmus agassizi*, which has also been reported in Ionian sediments of the eastern Ionian Sea (Agiadi et al., 2010) and the late Zanclean of Crete (Agiadi et al., 2013), is found again in the Calabrian (Kallithea section; sample Kal6), but is seems to be absent in coeval sediments of the western Mediterranean.

Gadidae are present in the record with four species: *Gadiculus argenteus*, *G. labiatus*, *G. thori* and *Micromesistius poutassou*. *Gadiculus argenteus* and *M. poutassou* still occur in the Mediterranean and have been present since the Tortonian (Lin et al., 2017a) and the early Pliocene (Girone, 2007), respectively. At present, *Gadiculus thori* is distributed at cold-temperate and subpolar latitudes of the Northeast Atlantic, and off Southeast Greenland, whereas *Gadiculus argenteus* occurs in warm-temperate water of the East Atlantic and the Mediterranean Sea (Gaemers and Poulsen, 2017). Fossil otoliths show that both species often co-existed in the Mediterranean from the Gelasian to the Calabrian (Girone et al., 2006a,b). However, the resolution in the present study allows us to infer that this coexistence was not continuous throughout this time interval. On the other hand, *G. labiatus* also exhibits a continuous record from the Tortonian to the Calabrian.

Oblada melanura, *Pagellus* cf. *bogaraveo*, *Sardinella maderensis*, and *Lesueurigobius sanzi*, already known from the lower Pliocene of the western Mediterranean, are reported here for the first time in the eastern Mediterranean outside the Ionian Sea. *Gobius* cf. *paganellus,* known in the eastern Atlantic from the Pliocene (Nolf and Marques Da Silva, 1997), and *Pagrus pagrus* are also reported in the eastern Mediterranean for the first time here. Finally, the discovery of *Lesueurigobius sanzi* at Kallithea constitutes its first record in the Calabrian of the eastern Mediterranean.

Looking at the stratigraphic distribution of extant taxa (at species or genus levels) that characterized the Miocene–Pliocene fauna but have abandoned the Mediterranean Sea today, it is possible to observe that some of them survived later in the eastern rather than in the western Mediterranean. These are usually cosmopolitan taxa of worldwide distribution such as *Scopelarchus analis, Benthosema suborbitale, Scopelopsis*, and *Laemonema*. One hypothesis, therefore, is that the continued restriction of the Mediterranean coupled with the Pleistocene climatic cooling led to the local extinction of these taxa in the western Mediterranean, whereas the eastern Mediterranean formed a refuge for warm-water species until the Late Pleistocene. Furthermore, during the Middle–Late Pliocene, an eastern Mediterranean–Red Sea connection was established through the Gulf of Aqaba on the Dead Sea Fault Zone (Popov et al., 2006). Meriç et al. (2016) showed that this connection was maintained until the Late Pleistocene, and

therefore offers another possible explanation for the large abundance of cosmopolitan fish in the eastern Mediterranean. It may also explain the complete extinction of typical Miocene–Pliocene species that had remained until that time, whose extant closest relatives however are not found today in the Mediterranean, such as *Scopelopsis pliocenicus*. On the other hand, regarding *Verilus mutinensis*, the only member of Acropomatidae living today in the Mediterranean Sea is *Synagrops japonicus*, which recently invaded the basin through the Suez Canal (Ambrogi, 2002; Arndt and Schembri, 2015; Hannachi et al., 2015). The genus *Verilus* is only found today in the Atlantic, although its extinct representative *Verilus mutinensis* was an eastern Atlantic–Mediterranean species (Schwarzhans and Prokofiev, 2017). The prevalence of this species in the Pleistocene of the eastern Mediterranean cannot be explained through any ephemeral connection with the Indian Ocean, and therefore supports the idea that the eastern Mediterranean functioned as refuge for warm-water species until the Late Pleistocene. As for *S. pliocenicus*, the only extant member of *Scopelopsis* is *S. multipunctatus*, which occupies the southern oceans. Therefore, the Pleistocene climatic deterioration and the final disconnection of the Mediterranean from the Red Sea may have led to the local extinction of these species during the Late Pleistocene. The present-day fish fauna of the southeast Aegean is however strongly affected by the alien species invasion from the Red Sea (Tserpes et al., 1999; Keskin et al., 2011; Corsini-Foka et al., 2017; Peristeraki et al., 2017). Comparing the modern situation with the Pleistocene in our study area confirms prevailing hypothesis (Belmaker et al., 2013) that the phenomenon of the Lessepsian invasion is the combined effect of an open Mediterranean–Red Sea connection and climate change.

4.2. Remarks on the paleobathymetry of the Lindos Bay Formation

The present paleodepth estimates based on the fish otoliths (Fig. 2) are compared with those of previous studies for the same sediments. The Lindos Bay Formation transgression reached a maximum that is estimated at 475 m and 400 m in the Cape Vagia section and the Kallithea road section, respectively. Titschack et al. (2013), based on biofacies analyses, showed that deposition of the upper part of the Lindos Bay Formation at Lardos occurred between 320 m (at least >150 m; lower part of the section), and approximately 100 m (upper part of the section). They attributed this rapid shallowing-upward trend to the tectonic uplift of Rhodes, as previously suggested by Van Hinsbergen et al. (2007). In addition, more recently, Milker et al. (2017) used a new benthic foraminifera-based transfer function to calculate the paleodepth of deposition of the Lindos Bay Formation for the interval 1.65–1.3 Ma. The results of the present study are in agreement with these previous estimates and indicate that the steep underwater topography, the active tectonic regime, as well as the recurrent sea-level changes continuously modified the composition of the fish fauna.

4.3. Taphonomy of fossil fish remains in the eastern Mediterranean

Here, we discuss certain taphonomic issues that arise in the study of fossil fish faunas, because these significantly affect paleoecologic and paleobiogeographic interpretations.

First of all, an important characteristic of the otolith assemblages in the studied sediments is the recurrent mixing of faunas, i.e., shallow-water taxa are often present along with deeper-water taxa in the same horizons. This is observed in sample Kal6 from the Kallithea road section and sample Lar3 from the Lardos section. This phenomenon may be related to the underwater topography of the study areas, where the depth gradient was high. Fish remains from rocky topographic highs and slopes were thus deposited and preserved in the depocenters of the submarine canyons, where sedimentation took place. This phenomenon, which appears commonly in fossil fish assemblages preserved in tectonically active areas (Agiadi et al., 2017; Karakitsios et al., 2017), is in agreement with the observations of Titschack et al. (2013), who reported thin fossiliferous debris flows in the Lardos section.

Secondly, plotting the species relative abundances per climatic group in the studied sections (Fig. 2), we observe a certain discrepancy just after the Gelasian/Calabrian boundary, during the MIS63 interglacial, as reflected in samples Vag3 and Kal2. In particular, sample Vag3 contains only one species, *Gadiculus labiatus*, which is an extinct species. Based on its widespread and continuous distribution in the entire Mediterranean from the Miocene to the Calabrian (Table 1), this species has been reasonably inferred to be a tropical species (Girone et al., 2006a,b). Therefore, the peak in the relative abundance of the tropical group in Vag3 (Fig. 2) may be artificial. In addition, sample Vag3 is the only sample taken from laminated marls deposited at a depth greater than 100 m, whereas sample Kal2 was taken from clayey limestones deposited between 100 and 200 m, and contains a much more diverse fauna, mainly subtropical (Fig. 2). At this point, the importance of resolution in the study of fossil fish assemblages should be stressed. Although, otoliths allow sampling entire geologic sections and constraining results in time, the quantity of sediment required is large and thus the resolution is dm-to-m–scaled and cannot be as high as for example that of micropaleontological studies. Conclusively, the observed discrepancy in this case may be an artifact of the sampling resolution and the different paleodepth and lithology of the two sites. For this reason, it would be unwise to produce a composite curve of the fish species relative abundances per climatic group, unlinked from the local conditions.

Furthermore, we notice significant differences between otolith-based and skeletal-based fossil fish records. A review of available data on the teleost fish taxa identified either through skeletal remains or otoliths in the south Aegean Sea and within Pliocene and Pleistocene sediments is shown in Table 2. A total of 90 species from 38 families have been identified; 69 species from 30 families have been identified based on their otoliths, whereas 20 species from 16 families have been identified based on the preserved skeletal parts. Only 3 species are commonly represented in the otolith and the skeleton-based records and only 8 families are reported by both. This comparison clearly demonstrates that the otolith-based record is much richer than the skeleton-based record. However, it must be noted that clupeids are especially favored in the skeleton-based record, in contrast to the otolith data, which is rather poor for this family, possibly because clupeid otoliths are very thin and fragile and therefore less commonly preserved in the sediments or after sampling and preparation procedures.

Fish skeleton preservation results in a restricted fossil record, because it requires specific conditions of deposition. On the other hand, otoliths can be preserved in a wider range of settings and thus allow us to reconstruct the evolution of the paleofauna more continuously. In their review of the skeletal remains versus the otolith record of the Messinian teleost fish, Girone et al. (2010) argued that: a) the skeletal fossil material has been studied far longer and more intensively than otoliths, and b) the otoliths found in situ are usually poorly preserved. These authors found great discrepancies between the otolith-based and skeleton-based faunas, at both generic and specific levels, and hypothesized the reasons behind them, such as the climatic latitudinal differences from south to north within the Mediterranean Sea. They further noted that otolith identifications had been much more up-to-date than those of the skeletal record in many occasions. The same observations apply to the Pliocene and Pleistocene eastern Mediterranean fish record.

Table 2
Comparison between the published skeleton-based versus the otolith-based record on the Plio-Pleistocene teleost fish fauna of the south Aegean Sea.

Family	Species		References
	Skeletal material	Otoliths	
Congridae		*Conger conger*	This study
		Gnathophis mystax	This study
		Pseudophichthys escavaratierensis	Agiadi et al., 2013
		Pseudophichthys splendens	Agiadi et al., 2013; This study
		Rhynchoconger pantanelli	Agiadi et al., 2013; This study
Engraulidae		*Engraulis encrasicolus*	This study
Clupeidae	*Alosa* cf. *elongata*		Gaudant 2001
	Alosa sp.		Gaudant et al., 1994
	Sardina cf. *pilchardus*		Gaudant 2001
	Sardina sp.		Gaudant et al., 1994
		Sardinella maderensis	This study
	Spratelloides gracilis		Gaudant et al., 1994; Gaudant and Symeonidis, 1995
	Spratelloides cf. *gracilis*		Gaudant 2001; Gaudant et al., 2010
Belonidae	*Belone* sp.		Gaudant et al., 1994; Gaudant 2001
Scomberesocidae	*Scomberesox* sp.		Gaudant et al., 1994; Gaudant 2001
Centriscidae	*Ampisile* cf. *strigata*		Gaudant 2001
Sygnathidae	*Syngnathus albyi*		Gaudant et al., 1994
	Syngnathus cf. *albyi*		Gaudant 2001
Argentinidae		*Argentina sphyraena*	This study
Gonostomatidae		*Gonostoma* sp.	This study
Sternoptychidae	*Maurolicus* cf. *muelleri*		Gaudant 2001
		Maurolicus muelleri	Agiadi et al., 2013; This study
		Polyipnus polli	This study
Phosichthyidae		*Vinciguerria attenuata*	This study
		Vinciguerria poweriae	Agiadi et al., 2013; This study
Chlorophthalmidae		*Chlorophthalmus agassizi*	Agiadi et al., 2013; This study
Scopelarchidae		*Scopelarchus analis*	This study
Myctophidae		*Benthosema glaciale*	This study
		Benthosema suborbital	This study
		Ceratoscopelus maderensis	Markopoulou-Diakantoni and Kagiouzis (2001); Lavorati, 2002; Agiadi et al., 2013; This study
		Diaphus aff. *adenomus*	Agiadi et al., 2013
		Diaphus cavallonis	Agiadi et al., 2013
		Diaphus holti	Lavorati, 2002; Agiadi et al., 2013; This study
		Diaphus rafinesquii	Agiadi et al., 2013; This study
		Diaphus aff. *splendidus*	Agiadi et al., 2013
		Diaphus taaningi	Agiadi et al., 2013; This study
		Electrona risso	Lavorati, 2002; This study
		Hygophum benoiti	Agiadi et al., 2013; This study
		Hygophum hygomii	Agiadi et al., 2013; This study
		Lampadena sp.	This study
		Lampanyctus crocodilus	This study
		Lobianchia dofleini	Lavorati, 2002; Agiadi et al., 2013; This study
		Myctophum fitchi	Agiadi et al., 2013
		Myctophum punctatum	Lavorati, 2002; This study
		Notoscopelus elongatus	Lavorati, 2002; This study
		Notoscopelus resplendens	Agiadi et al., 2013
		Protomyctophum arcticum	This study
		Scopelopsis pliocenicus	Agiadi et al., 2013; This study
Bregmacerotidae	*Bregmaceros albyi*		Gaudant et al. 1994
	Bregmaceros cf. *albyi*		Gaudant 2001
		Bregmaceros sp.	Markopoulou-Diakantoni and Kagiouzis, 2001; Agiadi et al., 2013

Family	Taxa		References
	Skeletal material	Otoliths	
Macrouridae		*Coelorinchus artinaberi*	Lavorati, 2002
		Coelorinchus sp.	This study
Moridae	*Gadella* sp.		Gaudant and Symeonidis 1995; Gaudant 2001
		Laemonema sp.	Agiadi et al., 2013; This study
Phycidae		*Phycis blennoides*	This study
Lotidae		*Gaidropsarus* sp.	This study
Gadidae		*Gadiculus argenteus*	Lavorati, 2002; This study
		Gadiculus labiatus	Agiadi et al., 2013; This study
		Gadiculus thori	This study
Gadidae		*Micromesistius poutassou*	Lavorati, 2002; This study
	Micromesistius sp.		Gaudant 2001
Ophidiidae		*Ophidion barbatum*	This study
		Monomitopus metriostoma	This study
Carapidae		*Carapus acus*	This study
		Echiodon dentatus	Agiadi et al., 2013; This study
Bythitidae		*Grammonus ater*	Agiadi et al., 2013; This study
Atherinidae		*Atherina boyeri*	Agiadi et al., 2013; This study

Table 2 (*continued*)

Family	Taxa		References
	Skeletal material	Otoliths	
Dactylopteridae	*Dactylopterus* sp.		Gaudant et al., 1994; Gaudant 2001
Scorpaenidae		*Scorpaena* sp.	This study
Acropomatidae		*Verilus mutinensis*	Agiadi et al., 2013; This study
Apogonidae		*Apogon* sp.	Agiadi et al., 2013; This study
Epigonidae		*Epigonus* aff. *denticulatus*	Agiadi et al., 2013
Serranidae	*Serranus* sp.		Gaudant 2001
Carangidae	*Caranx* sp.		Gaudant 2001
		Trachurus mediterraneus	Lavorati, 2002
	Trachurus sp.	*Trachurus* sp.	Gaudant and Symeonidis 1995; Gaudant 2001; This study
Sparidae	*Boops* cf. *boops*		Gaudant et al., 1994
	Boops sp.		Gaudant 2001
		Dentex sp.	This study
		Diplodus cf. *annularis*	This study
		Oblada melanura	Agiadi et al., 2013; This study
		Pagellus bogaraveo	This study
		Pagellus erythrinus	Agiadi et al., 2013; This study
		Pagrus pagrus	This study
Centracanthidae		*Spicara smaris*	This study
Cepolidae		*Cepola macrophthalma*	Agiadi et al., 2013; This study
Pomacentridae		*Chromis chromis*	This study
Blennidae		*Blennius ocellaris*	This study
	Blennius cf. *pavo*		Gaudant et al., 1994
Trichiuridae	*Lepidopus* cf. *caudatus*		Gaudant 2001
	Lepidopus sp.		Gaudant et al., 1994; Gaudant 2001
Scombridae	*Scomber* sp.		Gaudant 2001
	Scomberomorus sp.		Gaudant 2001
Gobiidae		*Aphia minuta*	Agiadi et al., 2013; This study
		Chromogobius zebratus	This study
		Deltentosteus quadrimaculatus	Agiadi et al., 2013; This study
		Gobius niger	Lavorati, 2002; Agiadi et al., 2013; This study
		Gobius cf. *paganellus*	Agiadi et al., 2013; This study
		Lesueurigobius friesii	Agiadi et al., 2013; This study
		Lesueurigobius sanzi	Agiadi et al., 2013; This study
		Lesueurigobius suerii	Agiadi et al., 2013; This study
		Pomatoschistus sp.	Agiadi et al., 2013
Citharidae		*Citharus linguatula*	Agiadi et al., 2013
Bothidae		*Arnoglossus kokeni*	Agiadi et al., 2013; This study
		Arnoglossus laterna	Lavorati, 2002

Considering the different ecological and facies parameters affecting fossil preservation, the Pliocene Voutes section on Crete (Agiadi et al., 2013) offers a good example. The diatomite beds cropping out in that section, which also contain skeletal remains, include otolith assemblages depleted in benthic and benthopelagic fish, but enriched in mesopelagic myctophids, gadids, and *Bregmaceros* sp. On the contrary, marl beds exhibit rich and well diversified faunas with species from levels of the water column, i.e., low stratification. The same phenomenon was observed by Girone et al. (2010) in the Tanaro section in Italy. There, articulated skeletons were found in laminated clays and diatomites, likely indicating anoxic or hypersaline conditions during deposition. The faunas, both skeleton-based and otolith-based found in laminated or diatomitic depositions, lack a strong benthic and benthopelagic component. On the contrary, otolith-based faunas identified within other types of sediments, are rather rich in bottom-dwelling fish.

Overall, fish skeletal material and otolith assemblages are complementary, in terms of both faunal reconstruction and their paleoenvironmental implications. Indeed, fish skeletons provide evidence about the fish taxa living in a particular locality, whereas otoliths enable a broader paleobiogeographic reconstruction, since, usually, otolith assemblages are richer. At the same time, seawater stratification and oxygenation conditions control the preservation of skeletal or otolith material, especially when it comes to bottom-dwelling species.

4.4. Long-term climatic changes impact on fish geographic distribution

In this part, we present the long-term trends in the Pleistocene Mediterranean fish assemblages as revealed by synthesizing the present results with those from previous studies, revealing patterns of species replacements and disappearances, and we further hypothesize on their causes and mechanisms.

The transition from the warmer Pliocene to an overall cooler Pleistocene climatic regime was transferred to the fish assemblages, through the replacement of pelagic tropical–subtropical by subtropical–temperate species (Girone et al., 2006a,b). Very characteristic is the example of the meso-bathypelagic genus *Notoscopelus*. Currently, subtropical species *Notoscopelus elongatus*, which is endemic to the Mediterranean, inhabits the Aegean Sea (Labropoulou and Papaconstantinou, 2000). Until recently, this species had been considered a subspecies of the North Atlantic temperate species *N. kroyeri* and often no distinction was made between the two variants. In the eastern Mediterranean, *N. elongatus* is believed to have occurred from the Gelasian to the present (Girone et al., 2006a,b). *Notoscopelus resplendens* has been identified since the Zanclean in the eastern Mediterranean (Agiadi et al., 2013). Girone et al., 2006a,b supported that *N. elongatus* s.l. (including *N. kroyeri* at that time) replaced the tropical-subtropical *N. resplendens*, which is today distributed worldwide in the tropical–subtropical extra-Mediterranean realm and very common

in the western Mediterranean assemblages from the Miocene to the middle Pliocene (Brzobohaty and Nolf, 1996; Nolf et al., 1998; Girone, 2007). Recently, Agiadi et al. (2017) and Lin et al. (2015, 2017a) documented the co-occurrence of *N. elongatus* and *N. resplendens* during the Tortonian, both in the eastern and western Mediterranean, suggesting that the migration into the Mediterranean of this temperate–subpolar Atlantic taxa started before the Plio-Pleistocene; during the Tortonian, the establishment of psychrospheric conditions (Benson, 1991) in the Mediterranean probably favored the migration of subpolar–temperate taxa such as *N. elongatus* s.l. from the Atlantic into the Mediterranean. Moreover, Girone et al., 2006a,b also reported *Notoscopelus (elongatus)* aff. *kroyeri* in the Calabrian sediments of Vrica and Fiumefreddo (Italy). Possibly, the different thermal gradient developed during the Plio-Pleistocene, between the two distribution-areas of *N. elongatus* s.l., in the North Atlantic and the Mediterranean, favored the differentiation of the two species (*N. elongatus* and *N. kroyeri*). *Notoscopelus kroyeri*, which is distributed today in the NE Atlantic, between the Arctic Circle and 37°N, invaded the Mediterranean only during colder Pleistocene intervals.

Tropically distributed pelagic taxa appearing throughout the Pliocene have now departed from the Mediterranean. Examples include *Bregmaceros* sp. (Agiadi et al., 2013), recently re-entering as *B. nectabanus* (Harold and Golani, 2016), as well as *Diaphus taaningi* (although its presence in the Mediterranean fossil record is under question based on the study of Schwarzhans and Aguilera, 2013), *Monomitopus metriostoma*, *Scopelarchus analis*, *Benthosema suborbitale*, *Diaphus adenomus* and *Diaphus splendidus*. *Myctophum fitchi*, presumably a subtropical (-tropical) species, was gradually replaced by the subtropical-temperate *Myctophum punctatum* in the meso-bathypelagic domain. Likewise, *Rhynchoconger pantanellii* is considered a subtropical – tropical species of the continental slope. During the Calabrian, the purely subtropical congrid *Gnathophis mystax* occupies this continental slope, possibly displacing *R. pantanellii*.

Interesting is the occurrence of *Chlorophthalmus agassizi* in Pliocene and Pleistocene deposits of the eastern Mediterranean. This species has never been reported in the western Mediterranean. Today, *Chlorophthalmus agassizi* dominates the eastern Ionian Sea, whereas *Gadiculus argenteus* prefers the western Ionian waters (Mytilineou et al., 2005). Anastasopoulou et al. (2006) suggested that *C. agassizi* is well adapted to oligotrophic environments, exploiting a wide variety of available niches. If indeed *C. agassizi* is an oligotrophy indicator, then its presence since the Calabrian, but also in the Zanclean (Agiadi et al., 2013), is very suggestive of the eastern Mediterranean oceanographic conditions at these times.

The results presented here indicate that climate changes had a direct and immediate impact on the fish faunal composition and the species abundances. Furthermore, they suggest that this effect was reversible to some extent. Nevertheless, after frequent and recurring environmental changes, the effect on the fish faunas was irreversible, i.e., fish species became locally extinct.

Several Miocene species were recorded in the Calabrian, such as *Scopelarchus analis, Gadiculus labiatus, Benthosema suborbitale, Diaphus taaningi, Pseudophichthys splendens, Verilus mutinensis, Lesueurigobius sanzi,* and *Arnoglossus kokeni*; they returned to the Mediterranean after the Messinian Salinity Crisis, but disappeared during the Late Pleistocene. The subpolar species *Protomyctophum arcticum* is reported here as a frequent cold-water guest in the Mediterranean during the Calabrian (1.37 Ma) and the Ionian (0.65 Ma). Also, cold-water *Gadiculus thori* was in the eastern Mediterranean at 0.79 Ma, along with *Gadiculus argenteus* and *Micromesistius poutassou*, possibly indicating climate deterioration. *Chlorophthalmus agassizi*, which inhabits only the eastern Mediterranean today and whose distribution is presumably associated with oligotrophy, continues to appear consistently in all eastern Mediterranean records from the Zanclean onward.

Overall, the eastern Mediterranean teleost fauna, during the Pleistocene, was not very different from the present-day one. Indeed, the neritic environment was inhabited by small pelagic fish such as anchovies (*Engraulis encrasicolus*), sardines (*Sardinella maderensis*) and horse mackerels (*Trachurus* sp.), and bottom-dwelling gobiids. *Sardinella maderensis* recruitment today follows upwelling patterns in the eastern Atlantic (Ba et al., 2016), whereas the distribution of *S. aurita* in the western Mediterranean and the Atlantic has been linked to climate oscillations (Sabatés et al., 2006; Zeeberg et al., 2008). Thus, it is reasonable to assume that *S. maderensis* found spawning grounds in the eastern Mediterranean during the latest Gelasian (sample Vag1) and the early Calabrian (sample Vag4).

Occasional euryhaline conditions allowed the establishment of an *Atherina* population. The pelagic domain contained a well-established and diverse mesopelagic fauna comprised mostly of Myctophidae, but also Gonostomatidae, Sternoptychidae, Phosichthyidae and Scopelarchidae. The deep-water fauna was quite diverse, comprising in most cases gadids (*Gadiculus* spp. and *Micromesistius poutassou*), but also congers, sparids and carapids.

Our data consequently show that the Pleistocene climatic deterioration has been reflected in the fish fauna, through multiple abrupt and gradual replacements in both the coastal-neritic and the pelagic assemblages. The functional classification approach attempted here reveals that tropical-subtropical pelagic-oceanic and mesopelagic taxa were replaced by subtropical-temperate fish. Changes in the neritic benthic community were rather rare, while the deep-water inhabitants exhibited great stability, with few gradual replacements taking place during the Pliocene and the Pleistocene, such as those of *Pseudophichthys escavaratierensis, Gadiculus labiatus,* and *Verilus mutinensis*.

4.5. Effect of Pleistocene climatic variability on the Mediterranean dispersal of marine fish

Today in the Mediterranean, the distributions of marine fish species are the combined result of warming climate, connectivity changes, and anthropogenic activity impacts (fisheries and habitat deterioration). However, during the Pleistocene, climate dominantly determined these distributions. Considering the intense and recurring climate changes that occurred during the Pleistocene, studying fish faunas from this epoch allows us to isolate the impact of climate change (Fig. 2). Here, we identify fish species invasions in the Mediterranean during the Pleistocene and correlate them with glacial and interglacial stages. Plotting the relative abundance of fish species grouped according to their climatic zone affinities, we correlate the presence and relative abundance of temperate and subpolar species with the Pleistocene MIS succession of Lisiecki and Raymo (2005).

In the Pleistocene, at Rhodes, the Gelasian and earliest Calabrian fish fauna are devoid of cold-water North Atlantic fish invasive species (Fig. 2). Such marine invasive species first occur from ~1.5 Ma during the Calabrian. In particular, in Vagia, we observe the invasion of the subpolar species *M. poutassou*, today absent from the eastern Mediterranean basin, along with a peak in the relative abundance of the cold-water mesopelagic species *B. glaciale* in sample Vag4, which apparently is correlated with MIS50 (1.51–1.492 Ma; Lisiecki and Raymo, 2005). According to Tzedakis et al. (2017), MIS52 marks the initiation of a gradual shift in higher energy required for deglaciation, leading to longer glacials. This increasing amplitude of glacial–interglacial fluctuations starting from MIS52 has been shown to correlate with significant increases in glacial ice volumes and ice-rafted debris in the North

Atlantic (Hodell and Channell, 2016), as well as decreasing sea surface temperature (SST) in the North Atlantic (Lawrence et al., 2010). After 1.5 Ma, during glacials, SST and zonal SST gradients in the subpolar North Atlantic decreased (Hodell and Channell, 2016). We propose here that, during these longer and more severe glacial periods after 1.5 Ma, some cold-water fish from the subpolar North Atlantic region extended their distribution southward and invaded the eastern Mediterranean. Other cold-water species invasions recorded here afterward are that of *M. poutassou* during MIS44 (Kallithea sample Kal6) and the *B. glaciale* peak during MIS36 (sample Kal7).

During the Ionian age, the studied interval at Lardos corresponds to the late MIS20 – MIS17 (Titschack et al., 2013), an interval which is characterized by important millennial and submillenial climatic fluctuations (Tzedakis et al., 2017). In the Ionian Sea, during late part of MIS20 (between 793.2 and 788.1 ka) a phase of polar-subpolar water incursion was reported and correlated to increasing aridity on land, recognized in the pelagic realm by the incursion at lower latitudes of left-coiling morphotypes of the planktonic foraminifer *Neogloboquadrina pachyderma* (Maiorano et al., 2016). This bioevent has been interpreted as the regional equivalent of the North Atlantic ice-rafted debris event, occurring close to the Termination IX (Wright and Flower, 2002; Kleiven et al., 2011). This period had a strong impact on the Mediterranean marine ecosystems. For example, in the central Mediterranean, ostracods and molluscs responded synchronously to climate change during MIS21–19 (Rossi et al., 2018). In the southeastern Aegean Sea, this marked cooling event characterized by decreasing SST apparently favored the invasion of the subpolar fish species *G. thori* and *M. poutassou* into the Mediterranean basin, as well as the abrupt increase in abundance of *Benthosema glaciale* (Figs. 2 and 6). Upward in the Lardos section, in levels correlating with the interglacial MIS19, the fish faunal diversity (as indicated by the number of species) and the number of individuals in the assemblages are significantly higher than in overlying levels correlated with MIS18. The assemblages during MIS19 show an increase in the abundance of temperate and subtropical taxa at the expense of subpolar species (Fig. 6). In particular, we notice an increase in extra-Mediterranean subtropical species, namely in the abundance of *D. taaningi* and the invasion of *P. polli.* Evidence of sea surface warming leading to the invasion of tropical–subtropical "guests" into the Mediterranean are found also at Montalbano Jonico (Italy, Ionian basin), where specimens of tropical–subtropical *Bonapartia pedaliota* are reported during a period of thermal maximum (Girone and Varola, 2001; Marino et al., 2015).

At Lardos, the increased relative abundance of subpolar species (including *P. arcticum*, *M. poutassou*, and *Benthosema glaciale*) and the absence of tropical species reflect the establishment of glacial

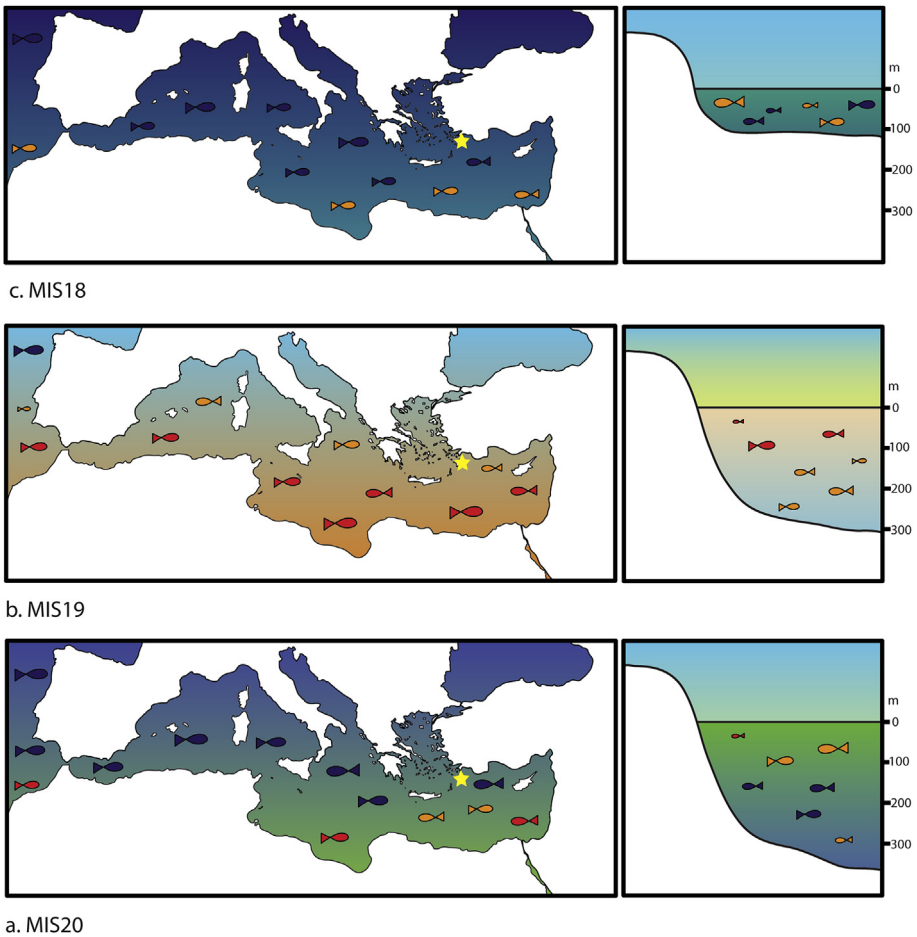

Fig. 6. Schematic model showing the effect of glacial–interglacial transitions on the Mediterranean fish fauna using the interval MIS20–MIS18 as an example (left panel) and local expression of these changes considering the estimated paleobathymetry off the eastern coast of Rhodes (right panel). Colored fishes: red – tropical species, orange – subtropical species, blue – temperate and subpolar species. Color gradient in map reflects roughly the SST changes during each time-period. In right panel, color gradients reflect roughly water and air temperatures during each time-period. Star indicates the location of Rhodes. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

conditions corresponding to MIS18 (Fig. 6). In addition, the MIS18 interval is characterized by the establishment of an *Engraulis encrasicolus* population, which is revealed during this interval because the study area has been significantly uplifted by that time (Figs. 2 and 6). The close link between climate and small pelagic fish populations has been historically observed, in seasonal to centennial time-scales (Finney et al., 2010; Alheit et al., 2014). The fossil record of *E. encrasicolus* so far indicates that this species first appeared in the Mediterranean after the Messinian salinity crisis (Girone et al., 2006a,b). Its modelled distribution, based on the IPCC A2 emissions scenario (Froese and Pauly, 2018), favors its expansion toward the western Mediterranean and the Atlantic coasts, and withdrawal from the eastern Mediterranean. Therefore, we speculate that the cool climate conditions occurring during MIS18 enabled this species to expand its distribution in the eastern Mediterranean, within the Ionian and the southern Aegean Seas.

Finally, the contribution of temperate and subpolar species dropped again during MIS17, while the abundance of subtropical taxa increased at Rhodes contemporaneously with a new invasion event of *P. polli* reported in the western Ionian basin (Girone and Varola, 2001).

5. Conclusions

In this study, we identified the marine fish fauna in Gelasian–Ionian shallow water to hemipelagic sediments of the northeastern coast of Rhodes in the eastern Mediterranean. The identified otolith assemblages were used to reconstruct the paleobathymetry of these deposits, based on the modern bathymetric distribution of the species and the occurrence of otoliths in surficial sediments of the Mediterranean. Mixed shallow-deep otolith assemblages are frequently recorded in the studied sediments, probably reflecting high bathymetric gradients and rapid bathymetric changes, as indicated by (Titschack et al., 2013). Furthermore, we examined and expanded the biogeographic and stratigraphic distributions of these species, and correlated their occurrences with specific glacial and interglacial intervals of the Pleistocene.

The eastern Mediterranean shelf environment maintained a mostly subtropical–temperate fish fauna during the Middle and Late Pleistocene, with a few tropical fish showing limited relative abundances in all assemblages. This fauna was punctuated by invasion events of cold-water fish species originating from the North Atlantic that were correlated here with the glacials MIS50, 44, 36, 20, and 18. The extripation of tropical species did not coincide with these intervals, but appears to have been independent of the introduction of cold-water species. Throughout the studied interval, warm-water species seem to have recovered after deglaciations, and indeed some species are found only in the eastern and not in the western Mediterranean. This suggests that the eastern Mediterranean acted as a refuge area for cosmopolitan tropical–subtropical species until the Late Pleistocene. The local extinction of these warm-water species in the Mediterranean may have been the combined result of the connection restriction of the Mediterranean with the Red Sea and the Late Pleistocene climatic deterioration due to longer and more pervasive glaciations.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at https://doi.org/10.1016/j.quascirev.2018.07.037.

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